SUCCESSION IN THE SWAMP FOREST FORMATION IN NORTHERN OHIO.*

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INTRODUCTION.

In descriptions of the deciduous swamp forest formation of eastern North America plant ecologists have generally recognized an elm-ash-soft maple† community. In Northern Ohio this community occurs in the successional series from both marsh and relict bog. In the succession from marsh it follows the willow-poplar association, and in the bog habitats of northeastern Ohio it succeeds the tamarack forest. The swamp forest formation is ultimately invaded and succeeded either by beech-maple of by oak-hickory when the habitat becomes adequately drained through filling or the development of drainage systems. Although the elm-ash-soft maple community has been long recognized, it has usually received but passing mention in the literature. Its composition, local and geographical variants, and its successional or transitional phases are inadequately described.

An attempt to map the forests of northern Ohio in considerable detail‡ led to the necessity of recognizing (1) certain successional or transitional phases of the swamp forest that frequently developed previous to the invasion of beech, hard maple, or white oak, and (2) certain swamp forest communities in which some of the characteristic secondary species of the elm-ash-soft maple community became sufficiently abundant to be classed among the principal dominants. Some of the data obtained are presented in this report partly because they are helpful in interpreting and classifying forest communities often encountered, and partly to suggest conditions and hypotheses that need further investigation.

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*Papers from the Department of Botany, Ohio State University, No. 262.

†The term soft maple is used in this paper to include both the silver maple (*Acer saccharinum*) and red maple (*Acer rubrum*). The term hard maple includes sugar maple (*Acer saccharum* and *A. saccharum* Rugelii) and black maple (*Acer nigrum*).

‡Sampson, H. C. and Transeau, E. N. Original plant associations as indices to biotic habitats with special reference to the corn borer. Ohio Agr. Exp. Sta. Bul. 429, pp. 152–163, 1928.

A chart showing the approximate habitat range and the order of invasion of trees into the swamp forest formation of northern Ohio is presented as a basis of showing more readily (1) the habitat range of species encountered in the swamp forest, (2) the order of invasion of the swamp forest habitat by the different tree species, (3) the transitional phases of the swamp forest, (4) the variations in relative abundance of individual species, (5) the different forest types encountered in the swamp forest formation, and (6) the relation of present secondary forests to the different phases of the virgin swamp forest.

In order that the reader may have a setting and a glimpse of certain major points that will be developed in this paper the following generalizations are stated at the outset. The commonly recognized elm-ash-soft maple community characteristic of swamp habitats in the Great Lakes region is often correctly designated as an american elm-white ash-red maple association in that these three trees are the dominant species. But in the wetter habitats occupied by the elm-ash-soft maple community, black ash is the species of ash encountered, and in northwestern Ohio silver maple is sometimes more abundant than red maple.

Of much more importance, however, are the two departures dependent upon the order of invasion and upon the variations in relative abundance of the secondary species of the elm-ash-soft maple community.

In the first place the order of invasion of the secondary species is dependent primarily upon drainage conditions. In the elm-black ash-soft maple association pin oak and swamp white oak are the principal secondary species. By the time the drainage is sufficient for white ash to appear as one of the dominants, bur oak and big shellbark hickory also come in as secondary species. With further increase in drainage several other secondary species come in, such as linden, black cherry, shagbark hickory, red and yellow oak, bitternut hickory, and even tulip and walnut. These secondary species are too rare in some localities to appear significant, but in other localities they are sufficiently abundant to attract attention and to suggest transitional phases of the elm-ash-soft maple community as indicated in the chart. The transitional phase characterized by tulip and walnut is not given special mention in the chart, but it is indicated by the length of the horizontal lines in the vertical column representing the red oak-linden transition.

Secondly, and still more important is the fact that some of these secondary species such as oaks, hickories, linden, tulip, and walnut may become so abundant in certain habitats that they are properly classed among the principal dominants of the forest community. In such habitats the expression "elm-ash-soft maple" is obviously a misnomer, and other forest communities corresponding to the transitional phases of the elm-ash-soft maple community mentioned above must be recognized. Terms used to designate these different forest communities are to be considered as tentative until further studies of the swamp forest formation are made. The term swamp forest formation is used in this paper to include the entire successional series of swamp forest communities.

Attention should be called to the fact that the swamp forest formation in northern Ohio is perhaps unexcelled anywhere in the northern and central portions of the Deciduous Forest Formation of North America both in area covered and in the number of tree species represented. It occupies much of the area within the old beach lines of the glacial lakes Maumee, Whittlesey, and Warren. It is the prevailing forest on that part of the old lake bed known as the Black Swamp of northwestern Ohio. On the glaciated area south of the beach lines it continues to be one of the prevailing forest types though seldom occupying large continuous areas. Owing to poor drainage many swamp forest habitats were the last to suffer the encroachment of civilization. Consequently conclusions reached in field surveys were checked by consulting men who knew the virgin forests of certain areas and were able to compare them with the present secondary forests, and with the few relict areas that have been least disturbed.

Of the upland forests of northern Ohio beech-maple is the most extensive and characteristic virgin forest. Of second importance are the white oak-black oak-hickory and the oak-chestnut communities. Other communities occurring locally are oak-chestnut-tulip, the mixed mesophytic forests, white pine, hemlock, beech-maple-hemlock-yellow birch, and big bluestem and bunch grass prairies.

On the old lake bed therefore are areas prevailingly swamp forest interspersed with local areas of beech-maple, oak-hickory, or marsh; areas prevailingly beech-maple interspersed with local areas of swamp forest and marsh; and areas prevailingly oak-hickory interspersed with local areas of swamp forest,

marsh, and prairie. The most extensive area of oak-hickory within the old beech lines is in Erie County.

The vegetation on the old beaches differs markedly in passing eastward across the state. In Fulton, Lucas, and Wood Counties White oak-black oak with some hickory is the characteristic forest of beach and sand deposits. In eastern Sandusky County beech and tulip are locally abundant on sand deposits, while in Erie County, oak-chestnut and oak-hickory occupy the sand and gravel deposits. From Berlin Township, Erie County, eastward oak-chestnut and oak-chestnut-tulip are on the dryest sand deposits, and beech-maple becomes one of the principal forests on the beach lines. In Ashtabula County, beech-maple-hemlock occurred locally.

On the morainal drift south of the old beach lines, the prevailing forest is beech-maple interspersed with numerous local areas of swamp forest. Locally areas of oak-hickory similarly interspersed with swamp forests are encountered.

ORIGIN OF THE SWAMP FOREST HABITATS IN NORTHERN OHIO.

The composition of the swamp forest is dependent in part upon previous vegetational history. The physiographic sites in which the swamp forest of northern Ohio has developed are old lake beds, flood-plains, and pre-erosion post-glacial flats. The vegetational history that preceded the swamp forest in each of these habitats may be summarized as follows:

In lake basins: (1) aquatic communities followed by communities characteristic of marshes and of wet prairie, (Jennings[1], Schaffner, *et. al.*[2]), (2) the willow-poplar association of low sand bars and beaches as they emerged (Jennings), and (3) the bog associations (Dachnowski[3], Transeau[4]).

On floodplains: (1) alder and willow-poplar associations, and (2) associations of stream valley bogs characteristic of the Northern Evergreen Forest Formation.

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[1]Jennings, O. E. An Ecological Classification of the Vegetation of Cedar Point. The Ohio Naturalist, 8: 291–340, 1908.

[2]Schaffner, J. H., Jennings, O. E. and Tyler, F. J. Ecological study of Brush Lake. Proc. Ohio State Acad. Sci., 4: 151–165, 1904.

[3]Dachnowski, Alfred. Peat Deposits of Ohio. Bull. 16, Geol. Survey of Ohio, 1912.

[4]Transeau, E. N. On the geographical distribution and ecological relations of the bog plant societies of northern North America. Bot. Gaz., 36: 401–420, 1903.

On certain pre-erosion post-glacial flats the deciduous swamp forest communities undoubtedly succeeded forest communities of the northern evergreen forest, such as spruce, balsam, arbor vitae, birch, and probably hemlock and white pine during the later post-glacial migration.

In addition to the natural successions noted above the influences of man have resulted in secondary successions of swamp forests following the clearing of beech-maple on moist uplands, and of bog shrubs and conifer forests in relict bogs.

The virgin swamp forests of Ohio have, therefore, succeeded the pioneer communities of three different climatic plant formations: (1) the bog heath and the bog conifer forest of the Northern Evergreen Forest Formation, (2) the associations of wet prairies, and (3) the vegetation of marshes characteristic of the Deciduous Forest Formation.

HABITAT RANGE OF THE SWAMP FOREST TREES IN NORTHERN OHIO, AND THE ORDER IN WHICH THEY INVADE THE SWAMP FOREST HABITAT.

Owing to the great number of tree species in the swamp forest a fairly definite knowledge of their individual distribution with respect to certain environmental factors is a valuable aid in recognizing the successional phases, and the variations in composition of different swamp forest communities. The accompanying chart made to illustrate certain facts of the behavior of trees as observed in the swamp forest formation of northern Ohio shows the relative distribution of the different swamp forest trees with respect to the combined effects of all the factors of the natural habitat, but it will be considered at first only to show (1) the approximate habitat range of each species that invades the swamp forest in northern Ohio, and (2) the relative order of the invasion of trees into the swamp forest habitat. The chart will be referred to later to illustrate the transitional phases of the elm-ash-soft maple community, the variations in relative abundance of the different species, and the consequent forest types of the swamp forest formation.

The horizontal lines in the chart indicate the approximate habitat range for each species. The habitat range was obtained in the field by using certain plant associations as habitat indices. The different species were first listed according to

Chart showing the approximate habitat range - horizontal lines - and the order of invasion of trees into the Swamp Forest Formation of northern Ohio. The pioneer shrub and tree communities of marshes and bogs which should appear on the extreme right of the chart are omitted. The relative abundance of species - when present - in the different phases of the plant communities cited in the chart is indicated by the following symbols: a = abundant, c = common, f = frequent, o = occasional, r = rare.

Species	Oak-Chestnut Community	Mixed-Mesophytic Community	Beech-Maple Association	Phases of the Elm-Ash-Soft Maple Community		
				Red Oak-Linden Transition	Bur Oak-Big Shell-bark Hickory Transition	Elm-Black Ash-Soft Maple Association
Acer saccharum Sugar Maple		r-a	f-a			
Quercus alba White Oak	r-a	r-a	r-c			
Fagus grandifolia Beech		r-a	c-a			
Magnolia acuminata Cucumber Tree	r-f	r-a	r-f	r-f		
Juglans nigra Black Walnut	r-f	r-c	r-c	r-a		
Juglans cinerea White Walnut	r-c	f-c	r-c	r-c		
Liriodendron tulipifera Tulip Tree	r-a	f-a	r-c	r-a		
Ostrya virginiana Hop Hornbeam	r-f	r-f	r-f	r-c		
Carya cordiformis Bitternut Hickory	r-f	r-f	r-f	r-c		
Quercus Muhlenbergii Yellow Oak	r-f	r-c	r-f	r-c		
Quercus rubra Red Oak	r-f	r-a	r-c	f-a		
Cornus florida Flowering Dogwood	f-a	c-f	r-f	c-f		
Carya ovata Shag-bark Hickory	r-c	c-f	c-c	f-a		
Morus rubra Red Mulberry	r-f	r-f	r-c	r-f		
Prunus serotina Black cherry	r-f	r-f	r-f	r-f		
Tilia americana Linden, Basswood	r-f	r-c	r-c	r-a		
Ulmus fulva Red Elm	r-f	r-c	r-f	r-c		
Gleditsia triacanthos Honey Locust			...	r-f	r-f	
Aesculus glabra Buckeye			..	r-f	r-f	
Quercus macrocarpa Bur Oak				r-a	r-a	
Carya laciniosa Big Shell-bark Hickory			...	r-a	r-a	
Carpinus caroliniana Blue Beech	r-c	r-f	r-f	f-c	f-c	
Fraxinus americana White Ash	r-c	r-a	r-c	r-a	c-a	
Platanus occidentalis Sycamore				r-f	r-f	r-f
Quercus palustris Pin Oak				r-f	r-c	r-a
Quercus bicolor Swamp White Oak				r-f	r-c	r-a
Nyssa sylvatica Sour Gum	r-f	r-f	r	r-c	r-c	r-a
Ulmus americana White Elm		r-f	r-c	c-a	c-a	c-a
Betula lutea Yellow Birch			r-f	r-f	r-c	r-a
Acer rubrum Red Maple	f-a	f-a	r-c	f-a	f-a	f-a
Acer saccharinum Silver Maple				r-a	r-a	r-a
Fraxinus nigra Black Ash				r-c	r-a	r-a
Populus deltoides Cottonwood				r-c	r-f	r-a

their occurrence or absence in certain plant associations known to represent different degrees of moisture and shade in the habitat. In northern Ohio, the oak-chestnut association* represents the dryest habitats, the willow-poplar association represents the wettest tree habitats, while the beech-maple association represents an intermediate condition of moisture and a maximum of shade. All tree habitats too wet for beech-maple but sufficiently drained for willow-poplar were considered as swamp forest habitats. Within each plant association a moisture gradient may also be recognized partly by the presence or absence of certain species and by the degree of exposure and of drainage associated with the topography and the composition of the soil.

The order of invasion of the trees into the swamp forest habitats is shown on the right side of the chart reading from the bottom of the page upward. The first nine trees at the bottom of the chart are shown extending to the limits of the chart on the right, since all of them invade either the pioneer willow-poplar or the tamarack forest neither of which are included in the chart, but may be assumed by the reader as placed to the right of the chart presented.

After the general habitat range of species with respect to plant associations was obtained, slope and the elevation of low ridges and knolls were then used as an index to the soil moisture gradient within the swamp forest habitat. To one unaccustomed to a flat landscape much of the old lake bed in Northern Ohio at first appears to be level. Closer observation and measurements, however, often show an abundance of low ridges and knolls with gentle slopes of but a few feet per mile. These rather slight differences in topography and consequent differences in surface drainage are reflected in the distribution of tree species. Many of these ridges are but a few inches to a few feet in height but often afford sufficient surface drainage for beech-maple or oak-hickory. On others different phases of the swamp forest are encountered. Internal drainage due to differences in soils was not measured, but soil differences, such as differences in amount of sand, muck, loam, and heavy clay, that could be readily recognized were noted. These marked differences in soils—with some exceptions for sand—appeared

*The oak-chestnut community as represented in the chart includes both the oak-chestnut association and the oak-chestnut-tulip association.

to have relatively little effect upon the *order of invasion* of wet habitats by most of the tree species. Variations in drainage on different areas of the same soil type may be great enough to encompass the whole order of invasion shown in the chart from the elm-black ash-soft maple association to the beech maple association. Furthermore the order of invasion of swamp forests by the principal tree species has been found to be consistent for hundreds of swamp habitats in central and northern Ohio and consequently upon many different soil types. As a result of the above observations, and since soil surveys of several counties in northern Ohio are now in various stages of completion it seemed advisable to postpone detailed studies of the effects of soil types until soil maps are available. Soil maps of Lake and of Sandusky County are now available, and a brief statement of the soil types of northern Ohio by Conrey* is also available.

Briefly, the order of invasion of the elm-ash-soft maple community by different species as drainage conditions increase was arrived at in the field (1) by listing the different species in the order of their invasion as one ascended a gentle slope from the edge of a marsh or lake or from the center of a depression within the swamp forest, (2) by comparing the distribution of species on adjacent low knolls and ridges of slightly different elevation, but of similar soils, and (3) by comparing the distribution of species on gentle slopes of similar soils, but varying in grade from slopes of one or two feet per mile to several feet per mile.

Owing to the great number of species involved and to the high degree of sensitiveness of the trees to slight changes in drainage, consistent data for all species may be expected only when very gentle and uniform slopes are studied. If the slope is abrupt, sufficient space between critical moisture conditions is not available for a definite zonal grouping of all of the species and the order of invasion is obscured. Perhaps the most irregular conditions are encountered in swamp forests in which the area is dotted with numerous small elevations just large enough to support one or a few mesophytic trees. Any one of several mesophytic trees may occur on the different individual knolls resulting in a forest as a whole that is composed of a

*Conrey, G. W. Soil fertility and soil types as indices to biotic habitats. Ohio Agr. Exp. Sta. Bul. 429, pp. 163–168, 1928.

mixture of swamp and upland trees; a mixture that might readily be confused with the mixed mesophytic community.

Elevation above the lake may be ignored, since the angle of the slopes is more important than absolute elevation. In many swamp forest habitats an abrupt elevation of seven to ten inches gives sufficient local drainage for beech-maple or oak-hickory. On the other hand a slope of three or four feet per mile may lead to an elevation of several feet above the lowest depression yet not be sufficiently drained for beech-maple. Consequently when drainage conditions and tree distribution on low knolls and ridges of slight differences in elevation are compared these elevated areas should be near one another, and both slope and kind of soil should be considered.

Locally, knolls of a few yards or a few rods in extent may be so abundant in a swamp habitat as to permit the development of mosaic forests consisting of a continuous swamp forest dotted with small island-like groves of forest types characteristic of better drained areas. The knolls may be composed of sand or of loams.

The order of invasion of the species into the swamp forest as shown to the right of the beech-maple in the chart is dependent upon their endurance of poor drainage or lack of soil aeration. The dropping out of several of these species and the decreased abundance of others when the habitat becomes better drained and is invaded by beech and hard maple is apparently the result of starvation in the dense shade of the latter species, since many of the swamp forest species grow abundantly as secondary forests in these habitats when beech-maple has been removed by clearing or when light is allowed to penetrate the forest canopy by the removal of one of the older trees. The order of dropping out of species as shown to the left of the beech-maple in the chart is dependent upon their endurance of desiccation. It appears that the major controlling factors of the external environment are the combined effects of light, moisture gradient, and soil aeration.

The data in the chart are based upon hundreds of field observations in the least disturbed areas now available. All of the species recorded were not sufficiently abundant in single habitats to determine their order of endurance of poor drainage. Hence each species had to be checked against another time after time in numerous habitats until the order of the whole series was determined. Most attention was given to the

limitations of species considered most significant for the region. The rare occurrence of some of the secondary species in all habitats leaves some doubt of the accuracy of the limitations indicated for them in the chart. A few secondary species are omitted from the chart, but are listed in the body of the paper. The limits of the habitat range indicated on the left side of the chart are based upon fewer data than those on the right.

While the chart is subject to refinement by further observation, by physical determinations of the soil moisture gradient at different seasons, and by experimental tests, it is sufficiently accurate to furnish a basis for the interpretation of the successional or transitional phases of the swamp forest in northern Ohio, and also for certain variations in both virgin and secondary forests.

SUCCESSIONAL OR TRANSITIONAL PHASES OF THE ELM-ASH SOFT MAPLE COMMUNITY.

In swamp habitats where the increase in drainage and soil aeration is very gradual certain successional phases of the elm-ash-soft maple community become evident. In the wettest habitats it is an *Ulmus americana—Fraxinus nigra—Acer rubrum* or *Acer saccharinum* swamp forest community. The secondary species when present in this first phase are sour gum, yellow birch, swamp white oak, pin oak, sycamore, cottonwood, black willow (*Salix nigra*), peach-leaved willow (*Salix amygdaloides*), and trembling aspen (*Populus tremuloides*).

As already pointed out in the introduction, transitional phases of the elm-ash-soft maple community may develop as a result of the order of invasion of its secondary species. Hence a second phase of the elm-ash-soft maple community is recognized when sufficient drainage exists for the entrance of white ash, big shell bark hickory, and bur oak apparently in the order named. There appears to be little difference in the endurance of poor drainage by these three species in natural habitats. Even with the entrance of these species the swamp forest usually remains an elm-ash-soft maple forest and is correctly designated the *Ulmus americana—Fraxinus americana—Acer rubrum* association, though in certain habitats the oaks and hickory also become prominent species. In secondary forests the prominence of oaks and hickory is not unusual. This phase of the swamp forest occupies a sufficient area of

gentle slopes in northwestern Ohio to deserve recognition. For convenience of reference this phase of the swamp forest may be designated the bur oak-big shellbark hickory transition, with the understanding that the name merely refers to the fact that drainage has become sufficient for these two species.

Certain other species also come into this phase of the swamp forest. Carpinus is usually present. Buckeye, honey locust, box elder (*Acer negundo*) and hackberry (*Celtis occidentalis*) are more infrequent in occurrence.

Still a third phase of the elm-ash-soft maple forest becomes evident when increased drainage has made possible the entrance of red elm, linden, cherry, mulberry, shagbark hickory, flowering dogwood, red oak, yellow oak, bitternut hickory, and hop hornbeam. Even with the entrance of these trees elm may continue to be the most abundant tree and many communities may be appropriately designated an elm-ash-soft-maple community or association. But the large number of species now present makes possible several variations in composition and, as will be shown later, in certain habitats the oaks and hickories also become prominent. Perhaps the most convenient name for this phase of the elm-ash-soft maple community is the red-oak-linden transition, with the understanding that the name does not necessarily refer to the prominence of these species but to the fact that drainage has become sufficient for them.

Additional species that may be found in this phase of the swamp forest are green ash (*Fraxinus lanceolata*), blue ash (*Fraxinus quadrangulata*), red ash (*Fraxinus pennsylvanica*), Kentucky coffee tree (*Gymnocladus diovica*), mockernut hickory (*Carya alba*), and fire cherry (*Prunus pennsylvanica*). In northeastern Ohio hemlock occurs sometimes as a relict in this phase of the swamp forest.

Still a fourth phase of the elm-ash-soft maple community sometimes becomes evident before invasion by beech, hard maple, or white oak. Its existence is dependent upon the entrance of tulip, white and black walnut, and magnolia into the swamp forest slightly before the invasion and dominance by beech. In this transitional phase of the swamp forest may be found individuals of all of the species named above, yet in many habitats elm-ash and soft maple may be the most prominent trees. In keeping with the terminology already used for the other phases of the swamp forest, this final phase may be designated the tulip-walnut transition.

The last three phases of the swamp forest are not always evident in a particular site. They may be evident on low ridges of slightly different elevation, in shallow depressions of different depths and degrees of drainage, and on very gentle slopes, but if the slope from the swamp forest to the upland forest is noticeably abrupt the assortment of the above species in the narrow fringe of forest at the edge of the swamp is not evident. Neither is it evident in swamp forests dotted with, numerous knob-like elevations upon which only one or two of the more mesophytic trees may grow.

While the above observations were made mainly upon swamp forest habitats that originated in marshes additional observations show that similar conditions exist in swamp forests originating in conifer bogs, and on flood plains. In fact the mixed forests on some of the flood plains of this region are more readily comprehended in the light of the facts stated above. These transitional phases may occur either where beech-maple or where oak-hickory is the upland forest. They also occur in the very numerous local swamp forest habitats in the beech-maple or oak-hickory forests on the glacial morain south of the old beach lines. Here the relative depth and drainage of the different depressions are at once characterized by the one or the other of the above transitional phases of the elm-soft-maple community, or by the corresponding forest community to be described under the following topic.

SWAMP FOREST COMMUNITIES RESULTING FROM VARIATIONS IN THE RELATIVE ABUNDANCE OF THE SECONDARY SPECIES OF THE ELM-ASH-SOFT MAPLE COMMUNITY.

As already pointed out the elm-ash-soft maple community may include an elm-black ash-red or silver maple association and the succeeding elm-white ash-red maple association. The latter association may further be considered in certain habitats as consisting of at least three transitional phases depending upon the order of invasion of its prominent secondary species. We come now to a brief consideration of a more fundamental modification of this association brought about by the relative increase in abundance of some of the secondary species that places them among the dominants of certain habitats. The resultant swamp forest communities correspond, in the suc-

cessional series, to the transitional phases of the elm-ash-soft maple community already described, but they are not dominated solely by elm, ash, and maple. In fact some of the secondary species may be more abundant than either ash, maple, or elm.

Attention is again called to the chart in which the relative abundance of species in different habitats is indicated by the following symbols: a = abundant, c = common, f = frequent, o = occasional, r = rare to absent. Two letters are used for each species since a considerable variation in the relative abundance of individual species is found when hundreds of observations are made. The letters refer to the relative abundance of the species in the virgin forests.

In the vertical column representing the elm-black ash-soft maple association yellow birch, pin and swamp white oak are recorded as rare to abundant. From the data at hand it appears that these oaks were usually only rare to frequent secondary species in the elm-ash-soft maple community of northern Ohio, and that the yellow birch was entirely absent in the swamp forests of northwestern Ohio.

In the column representing the bur oak-big shellbark hickory transition, or the wetter phase of the elm-white ash-red maple association, bur oak and big shellbark hickory are recorded as rare to abundant. They reached their greatest abundance in the swamp forests of northwestern Ohio.

In the column representing the red oak-linden transition, or the better drained phase of the elm-white ash-soft maple community, many secondary species are recorded. Several of these species frequently become abundant in this phase of development of the swamp forest formation in northern Ohio; principally red oak, shagbark hickory, linden, bur oak, and big shellbark hickory; while yellow oak, red elm, and bitternut hickory became conspicuous secondary species. In the best drained phases of the swamp forest formation tulip and walnut become abundant enough in certain habitats to be classed with the dominants.

This variation in relative abundance of species results in the development of several forest communities in the swamp forest formation. Which of these communities are extensive enough to be recognized and named? What are the most appropriate names for them? Satisfactory answers to these questions may be obtained only by a combined study of the

records of early surveys and present field studies, including inquiry among men who removed the virgin forests.

Sears* has studied the early surveyor's records of this region but his published data while helpful are too generalized to aid in the solution of some of the problems. Data from all of these sources were brought together in the present survey, but so much more remains to be done that only tentative answers may be proposed for the above questions at the present time.

The local abundance of yellow birch in the elm-black ash-red maple association in northeastern Ohio occurs in those habitats, principally bogs, that were dominated by communities of the Northern Evergreen Forest Formation until very recent times. The elm-black ash-red maple-yellow birch community, therefore represents a particular transition in the succession from the Northern Evergreen to the Deciduous Forest Formation.

Excessive abundance of pin oak and swamp white oak in the virgin forests of northern Ohio seems to have been quite local and probably associated with the occurrence of heavy clay soils. A pin oak type is already recognized by foresters, and it is perhaps sufficient merely to recognize that transitions may exist between the pin oak community and the elm-ash-soft maple community.

Bur oak was an important secondary species in the virgin elm-ash-maple community in northwestern Ohio. Much of it was cut for the building of ships in the early days of settlement. The area over which bur oak should be classed as a dominant along with elm, ash, or big shellbark hickory is undetermined. Perhaps this community is not extensive enough to deserve a special name except as a local variant, since a bur oak-elm association that succeeds wet prairie is already recognized.

Owing to the great number of species involved a much more complex situation is met when the forest communities corresponding to the red oak-linden transition in the successional series are considered. Since several of these secondary species of the elm-ash-soft maple community may occur as dominants in certain areas, several combinations of dominants are possible and several resultant forest communities may occur. Perhaps the most helpful classification of these communities will result from a general agreement among foresters and ecologists to

*Sears, P. B. The natural vegetation of Ohio. Ohio Jour. Sci. 25: 139–149, 1926. Ibid 26: 213–231, 1927.

choose one or two names such as red oak-linden-ash, red oak-linden-elm, or the mixed red oak-linden-ash community, that have a wide geographical significance and to consider the remaining combinations wherever found as variants. For example, in certain habitats in Portage County, Ohio, one might recognize an elm-shagbark hickory-red maple variant of this community. The remaining species of the red oak-linden transition occur in this variant but are rather infrequent. As a result of this variant in the successional series before invasion and dominance by beech, wet beech forests with elm, hickory, and red maple as the principal secondary trees are sometimes found in Portage County. In some variants the oaks and hickories characteristic of the elm-ash-soft maple community are so abundant in the least disturbed swamp forest relicts in northwestern Ohio that the forests have the characteristic physiognomy of an oak-hickory association. They can be distinguished from the upland white oak-black oak-hickory association only by their species composition.

The climax of luxuriance is reached in the swamp forest formation when drainage becomes sufficient for tulip, walnut, and magnolia to intermingle with the other species of the elm-ash-soft maple community. In certain habitats where the soil is composed of sandy or gravelly loam, tulip and walnut may be as abundant as the other dominants of the forest community. In special habitats where several species of this tulip walnut transition become about equally abundant, and in which beech and maple have become fairly common as a result of further drainage, the resultant mixed forest community resembles the mixed mesophytic community that sometimes develops as a special transition between beech maple and oak-chestnut. But this point will receive further consideration in a later paper.

Local societies of single species also occurred in the virgin swamp forests of northern Ohio. The early settlers report small areas of almost pure stands of cottonwood, black walnut, sycamore, elm, tulip, hickory, and pin oak. Pure stands of cottonwood are reported occupying as much as forty acres. John Coutches reports a pure stand of walnut covering almost a section of land on the site now occupied by the Standard Oil Company in the eastern part of Toledo. "The soil contains much sand, and mushrooms (morels) grew abundantly. Walnut

was also exceedingly abundant on some of the floodplains rich in sandy or gravelly loams."

The types of variations in the swamp forest communities discussed above may be found within the limits of a single county. When observations are extended over a wider geographical range, variations resulting from the elimination of certain species are found. Such variations are illustrated in Ohio by the absence of hemlock, yellow birch, pine, and magnolia in the Black Swamp of northwestern Ohio, and by the absence of sweet gum and river birch in northern Ohio. When the area is extended to include the swamp forests of Kentucky and Arkansas, several other variations in floristic composition and in relative dominance are encountered.

FACTORS UNDERLYING THE RELATIVE ABUNDANCE OF SPECIES IN THE DIFFERENT SWAMP FOREST COMMUNITIES.

In the above topic attention was called to the increase in relative abundance of tulip and walnut upon sandy and gravelly loams and of pin and swamp white oak upon certain heavy clay soils. Earlier in the paper attention was called to the outstanding effects of moisture and soil aeration upon the habitat range of the various tree species in northern Ohio, and upon the order in which these trees invaded the swamp habitat. The effect of shade in habitats occupied by beech-maple is shown in the chart by the greater abundance of these species in habitats both too dry and too poorly drained for beech-maple. Similarly certain species of the swamp forest formation may overshade other swamp forest species and decrease their abundance in certain habitats.

While drainage conditions, soil aeration, and the complex of factors underlying geographical distribution may account for the presence or absence of a species in one or more of the communities that make up the successional series of the swamp forest formation in northern Ohio, the explanation of local variations in relative abundance of a species within a particular community, such as the red oak-linden transition, in which the given species normally grows must also take into account the influence of several other factors, such as biotic competition, pre occupation by approximately ecological equivalents, biotic history of the habitats, and time and rate of succession.

Soil types have been proposed as an explanation of the distribution and composition of plant communities. The study of the relations of vegetation types and soil types is a fruitful field of research, and soil maps are of great aid to the biologist in indicating where changes in vegetation types may be expected. The soil type as it is mapped, however, represents a complex of factors, and therefore may not be relied upon to delimit the particular factor or factors of most importance biologically. In previous reports* the writer called attention to the fact that the soil type alone may decidedly fail to account for either the composition or the distribution of plant communities. For example under natural conditions the plant communities of marsh and wet prairie, and the transitional phases and communities of the swamp forest formation occurred upon the same soil type—Clyde silty clay loam—within the limits of one county. Furthermore these different plant communities also occurred upon Newton clay loam, Newton silty clay loam, and most of them upon Brookston silty clay loam within the same county. It is obvious therefore that different vegetation types may occur upon the same soil type, and that the same vegetation type may occur upon several soil types. But if we study all of these relations between a certain vegetation type and several soil types, the particular factors in the soil that influence the vegetation type may become evident.

SECONDARY SWAMP FOREST COMMUNITIES.

Several factors determine the nature of secondary swamp forests. Secondary forests may be little different from the virgin forests. Many of the secondary swamp forests of northern Ohio are claimed by the early settlers to be good examples of what grew there originally. Again secondary forests may consist mainly of secondary species of the virgin forest either in pure or mixed stands. This last condition may occur following a single clearing, but it is more likely to occur following repeated clearings or when grazing or cultivation intervenes between clearing and reforestation. Attention should also be called to the fact that numerous areas in the state now

*Sampson, H. C. Vegetation types and soil types of Marion County, Ohio. Ann. Assoc. Amer. Geog. 20: 40–41, 1930. Advantages and limitations of the use of the distribution of soil types as a basis of mapping the distribution of vegetation types. Proc. Ohio Acad. Sci. 40: 390–391, 1930.

occupied by secondary communities of swamp forest species were originally covered by beech-maple forests.

A comprehensive survey of secondary forests remains to be made. Attention, however, may be called to the relation of secondary swamp oak-hickory forests to the transitional phases of the swamp forest in northern Ohio. Beginning with the wettest phases of the elm-black-ash-soft maple community, the corresponding secondary swamp oak-hickory forest that may occur is given to the right in the following summary. The number of species of oak and hickory increases with each successive phase since species of the wetter phases still persist in the better drained phases.

Successional Phases of the Virgin Elm-Ash-Soft Maple Community:	Corresponding Secondary Swamp Oak-Hickory Forests:
1. Elm-Black Ash-Soft Maple Association.	Pin Oak-Swamp White Oak.
2. Bur Oak-Big Shellbark Hickory transition.	Bur Oak-Shellbark Hickory with Pin Oak, and Swamp White Oak.
3. Red Oak-Linden transition.	Red Oak-Hickory. Pin, Swamp White, Bur, and Yellow Oaks. Shellbark, Shagbark, and Bitternut Hickories.
4. Tulip-Walnut transition.	Similar to the one above.

The order of invasion of the swamp forest by beech and white oak is variable. Beech is usually first but not always. Beech is decidedly an earlier invader than hard maple. When a wet beech-maple forest is cleared the corresponding secondary oak-hickory forest which sometimes follows includes white oak in addition to the oaks listed above. The white oak-black oak hickory and the oak-chestnut-hickory association are characteristic of upland not of swamp habitats.